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Research Article

Tarachoptera: The extinct and enigmatic cousins of Trichoptera and Lepidoptera, with descriptions of two new species*

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Abstract

Two new species of fossil Tarachoptera are described from Burmese amber and named as *Tarachocelis emmarossae* **sp. nov.** and *Kinitocelis patrickmuelleri* **sp. nov.** The new species are documented by photos and line drawings. An update of the hitherto described taxa of Tarachoptera is provided including information about the depository of type material. The phylogenetic position of Tarachoptera in the amphiesmenopteran clade is discussed. A hypothetical cladogram based on cladistic principles was constructed to demonstrate the phylogenetic relationship combining Tarachoptera, Trichoptera, and Lepidoptera. It might serve as guidance in the interpretation of fossil taxa and future discoveries.

Key Words

Amphiesmenoptera, checklist, Cretaceous, fossil taxa, phylogeny, taxonomy

Introduction

During the 14th International Symposium on Trichoptera in Vladivostok in 2012, the first author discussed a fossil insect in a presentation which was not included in the program or printed in the abstract booklet. Furthermore, it did not find its way into the proceedings volume. It was the last scientific talk of the symposium on the last day and was a so-called progress report. With just three slides the presentation was relatively short, which was in strong contrast to the long, subsequent discussion. Five years later, after intensive study of the scattered paleontological literature, we were convinced of the amphiesmenopteran nature of this unusual and hitherto undescribed insect and decided to publish the results of our investigations.

At the "7th International Conference on Fossil Insect, Arthropods and Amber", which took place at the National Museum Scotland, Edinburgh, in 2016, we gave a talk about this fossil insect and established the family Tarachocelidae (Mey et al. 2017b). The new family was placed as Amphiesmenoptera incertae sedis. The most conspicuous character is the presence of scales covering parts of the wings, which also occur on the head and thorax. At that time, we were inclined to group the fossil closer to Lepidoptera than to Trichoptera, based on the presence of wing scales alone. We checked the paleontological literature and were unable to find similar or related taxa in the fossil record of Trichoptera and Lepidoptera. A little later, we received further fossil material from Burmese amber, which contained new and better-preserved specimens, allowing a more detailed

* The paper is part of 17th International Symposium on Trichoptera, Edited by Simon Vitecek, Astrid Schmidt-Kloiber, Wolfram Graf, Hans Malicky.

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Table 1. Revised checklist of genera and species of Tarachoptera known by 2023 and depository of type specimens (CNU – Capital Normal University, Beijing; MfN – Museum für Naturkunde, Berlin; NIGP – Nanjing Institute of Geology and Palaeontology, Nanjing; NMS - National Museum of Scotland, Edinburgh; ZFMK - Zoological Research Museum Alexander Koenig, Bonn).

Tarachoptera taxa	inventory no.
***Tarachocelis* Mey, Wichard, Müller & Wang, 2017a**	
T. microlepidopterella Mey, Wichard, Müller & Wang, 2017a	
Holotype, male	NMS-G2010.20.36
T. emmarossae sp. nov.	
Holotype, male, Paratype, female	ZFMK-TRI000837
***Kinitocelis* Mey, Wichard, Müller & Wang, 2017a**	
K. brevicostata Mey, Wichard, Müller & Wang, 2017a	
Holotype, female	MfN-MB.I.7323
Paratype, male	NIGP-164786
Paratype, female	NIGP-164787
Paratype, male	NIGP-164788
Paratype, male	coll. P. Müller
Paratype, male	coll. W. Wichard
K. dashengi Wang, Zhang, Engel, Sheng, Shih & Ren, 2022	
Holotype, male	CNU-TAR-MA 2015502
K. divisonotata Mey, Wichard, Müller & Wang, 2017a	
Holotype, female	NIGP-164789
Paratype, female	NIGP-164785
Paratype, female	NIGP-164787
Paratype, male	MfN-MB.I.7289
Paratype, male	coll. P. Müller
K. hennigi Mey, Wichard, Müller & Wang, 2017a	
Holotype, female	NIGP-164790
K. macroptera Mey & Wichard, 2020	
Holotype, male	MfN-MB.I.7341
K. patrickmuelleri sp. nov.	
Holotype, male	ZFMK-TRI000838
K. sparsella Mey, Wichard, Müller, Ross & Ross & 2018	
Holotype, male	MfN-MB.I.7284
K. sp. A (undescribed)	ZFMK
***Retortocelis* Wichard, Müller, Ross & Ross & 2018**	
Retortocelis longella Mey, Wichard, Müller, Ross & Ross & 2018	
Holotype, male	MfN-MB.I.7285
Retortocelis minimella Mey, Wichard, Müller, Ross & Ross & 2018	
Holotype, male	MfN-MB.I.7286
Paratype, male	MfN-MB.I.7287
Retortocelis spicipalpia Mey & Wichard, 2020	
Holotype, male	NIGP-170800
Paratype, male	MfN-MB.I.7342
Retortocelis tyloptera Mey, Wichard, Müller, Ross & Ross & 2018	
Holotype, male	MfN-MB.I.7288

study of these insects. They were identified as additional members of Tarachocelidae, albeit representing additional genera. Eventually, we became convinced that we should consider all these fossils assigned to Tarachocelidae to be representatives of a hitherto unknown order of insects, only distantly related to extant Lepidoptera and Trichoptera, and fossil Amphiesmenoptera. We established and described a new order and gave it the name Tarachoptera (Mey et al. 2017a). The name was derived from Greek and concerns the presumed staggering flight of the adults, which are minute insects with a wing-length from 2 to 5 mm.

In recent years, we published two subsequent papers providing descriptions of additional species and the erection of a third genus (Mey et al. 2018; Mey et al. 2020). A further species was recently described by Wang et al. (2022). Based on new material from Burmese amber, we describe two new species in the present paper.

Today, the order Tarachoptera is composed of one family, three genera and a total of 14 species (one of which is undescribed), including the two species described in the present article (Table 1). It seems to be a morphologically compact group. A summary of present knowledge was published by Wichard and Mey (2021). According to Wang et al. (2022) the position of Tarachoptera within the phylogenetic system of Holometabola is a sister group relationship to Trichoptera + Lepidoptera. Here, a somewhat different view about the phylogeny of Tarachoptera and its systematic position is presented.

Material and methods

The amber material was collected by local people in the Hukawng Valley of northern Myanmar (Myitkyina District, Kachin State) and derives from an amber-bearing layer which is not exposed to the surface but extends to a depth of 2–15 m (Cruickshank and Ko 2003).

The age given by UPb dating of zircons from the volcanoclastic matrix of the amber is early Cenomanian (98.8 ± 0.6 million years) (Shi et al. 2012).

The fossil specimens are embedded in small amber blocks cut from larger Burmese amber pieces. Photos were taken using a Leica stereomicroscope M 420 Apozoom in combination with a Canon EOS 600D, EOS utility software and the Zerene Stacker software or were taken by the digital microscope Keyence VHX-900F.

The fossils were examined under incident and transmitted light using a stereo microscope (Leica MZ125). Line drawings were produced with an attached drawing tube, and digitally processed using Adobe Photoshop CS4. Measurements were made with the ocular micrometer of the stereo microscope.

Systematic palaeontology

Order Tarachoptera Mey, Wichard, Müller & Wang, 2017a

Family Tarachocelidae Mey, Wichard, Müller & Wang, 2017a

***Kinitocelis* Mey, Wichard, Müller & Wang, 2017a**

Kinitocelis patrickmuelleri sp. nov.

https://zoobank.org//DFE7DCA8-D788-4792-B7FE-F1CBF5034281

Figs 1, 2, 6

Material. ***Holotype***, male, Burmese Amber, deposited in the Zoological Research Museum Alexander Koenig, Bonn, Germany, inventory no.: ZFMK-TRI000838 (ex coll. Patrick Müller, BUB 4498).

Preservation. The fossil is embedded in a flattened, oval piece of amber. The male is completely preserved, but in an unfavorable position with wings overlapping and covering the body (Fig. 6). Head, thorax, and abdomen partly macerated. Several air bubbles are present in the inclusion.

Etymology. The species is named in honor of Patrick Müller, collector and promoter of research on Burma amber inclusions.

Description. Length of body 2.2 mm, forewings 2.9 mm; head with a triangular, frontal process; eyes hemispherical; scape and pedicellus slender, not as broad as following flagellomeres (Fig. 1); 24 flagellomeres, broad, flat, quadrangular, with hairs or scales shorter than flagellomere diameter (Figs 6c, 6d).

Male genitalia (Figs 2, 6): dorsal plate long, tapering to round apex; ventral comb on sternum IX with 10 stiff spines.

Diagnosis. By using the identification key of Wichard and Mey (2021), the new species comes out as *Kinitocelis*. The new species can be distinguished from all congeners by the triangular, pointed anterior margin of the head and by the very broad flagellomeres of the antennae.

Tarachocelis Mey, Wichard, Müller & Wang, 2017a

Tarachocelis emmarossae sp. nov.

https://zoobank.org/A04E4D51-6DFA-40F4-A775-F61C3D2132AC

Figs 3–5, 7

Material. ***Holotype***, male, Burmese Amber, Paratype, female, included in the same amber piece, deposited in Zoological Research Museum Alexander Koenig, Bonn, Germany, inventory no.: ZFMK-TRI000837 (ex coll. Patrick Müller, BUB 4499).

Preservation. The fossils are embedded in a flat, oval piece of amber. The holotype is incompletely preserved (Fig. 7). Wings, genitalia and dorsal part of thorax and abdomen are missing. Legs and palps are macerated and hardly discernible. The female paratype is completely preserved, but in an unfavorable position with wings overlapping and kept close to the body. A third specimen is present in the piece, which belongs to an unidentified male *Kinitocelis* species.

Etymology. The new species is dedicated to Emma Ross, the first researcher examining the piece of amber containing the fossil that later became the first described species of Tarachoptera.

Description. Length of body 2–3 mm (male), forewings 2.5 mm (female); head elongate and somewhat flattened dorsoventrally, with anteriorly produced frontal part; eyes prolonged, nearly stalked, with apical rounded portion black (Fig. 3); antennae as long as body, scape longer than eye diameter, each flagellum with 23 flagellomeres, the terminal 6 or 7 flagellomeres thickened, the basal flagellomeres slender and long (Fig. 4); maxillary palps very short, each with three segments of equal length, last segment pointed; labial palps long, each with three segments, terminal segment longest, not enlarged apically; galea large, clavate, with six finger-like processes directed toward perioral opening.

Male genitalia (Figs 5, 7; macerated, not preserved): Ventral comb of sternum IX with 14 stiff and apically blunt spines. Legs with smaller spines on all tibiae, tarsal segments with terminal pair of ventral bristles.

Diagnosis. The species is unique in its clubbed antennae, a character encountered in Tarachoptera for the first time here and not observed in any other basal taxa. The anteriorly produced head is similar to *Tarachocelis microlepidopterella* Mey et al. (2017b), and based on this similarity and in the absence of other visible traits, the new species is assigned provisionally to *Tarachocelis*.

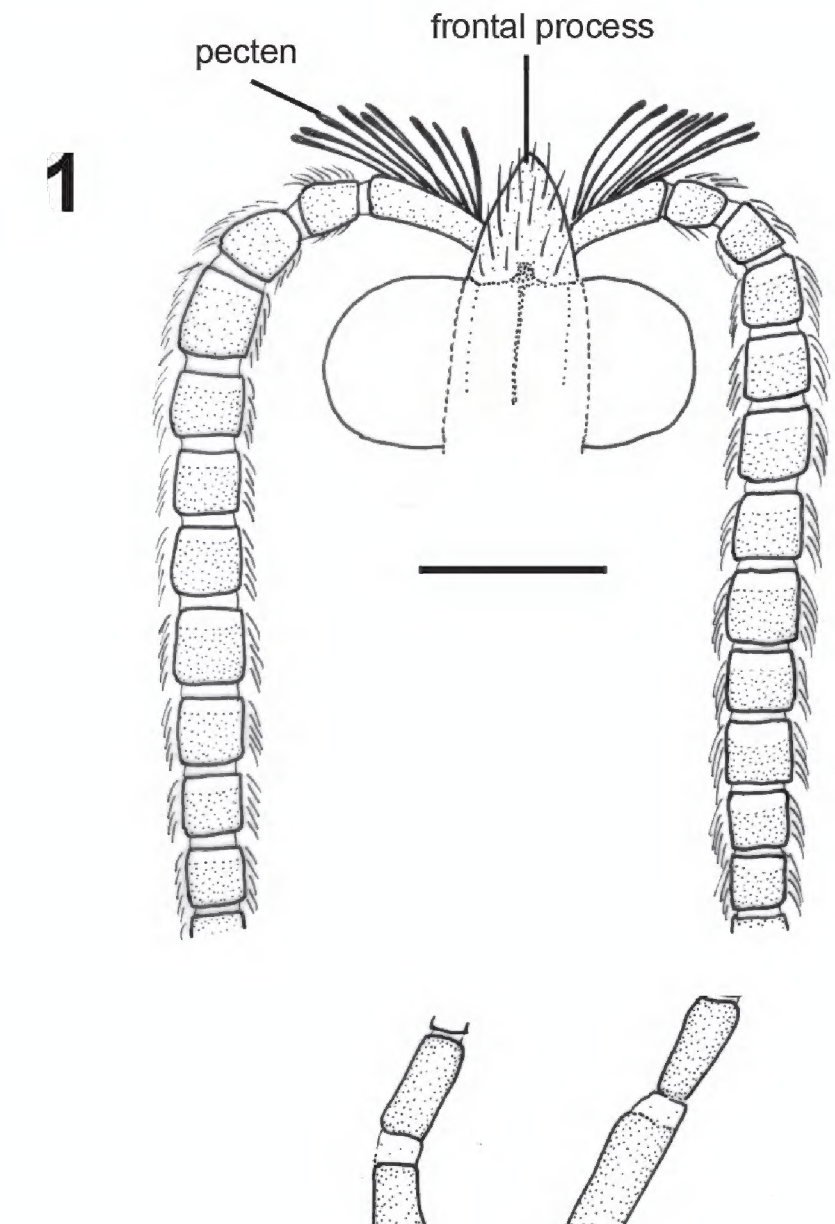
Results and discussion

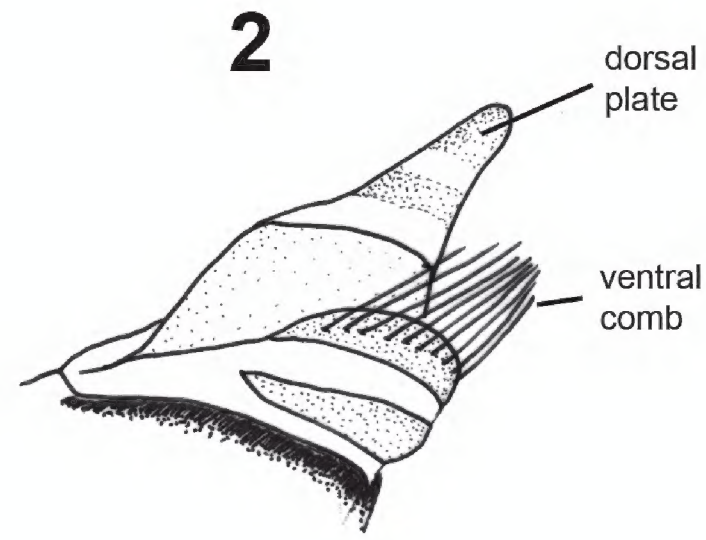
The two new fossil species provide new morphological characters, which were unknown from the hitherto described species. They considerably enlarge the spectrum of antennal morphology in the family Tarachocelidae and point to the significance of this character complex, which should be considered as a trait or expression of the still unknown biology of Tarachoptera. However, the new species do not bear any new clues, which could be used in the discussion on the phylogeny of Tarachoptera.

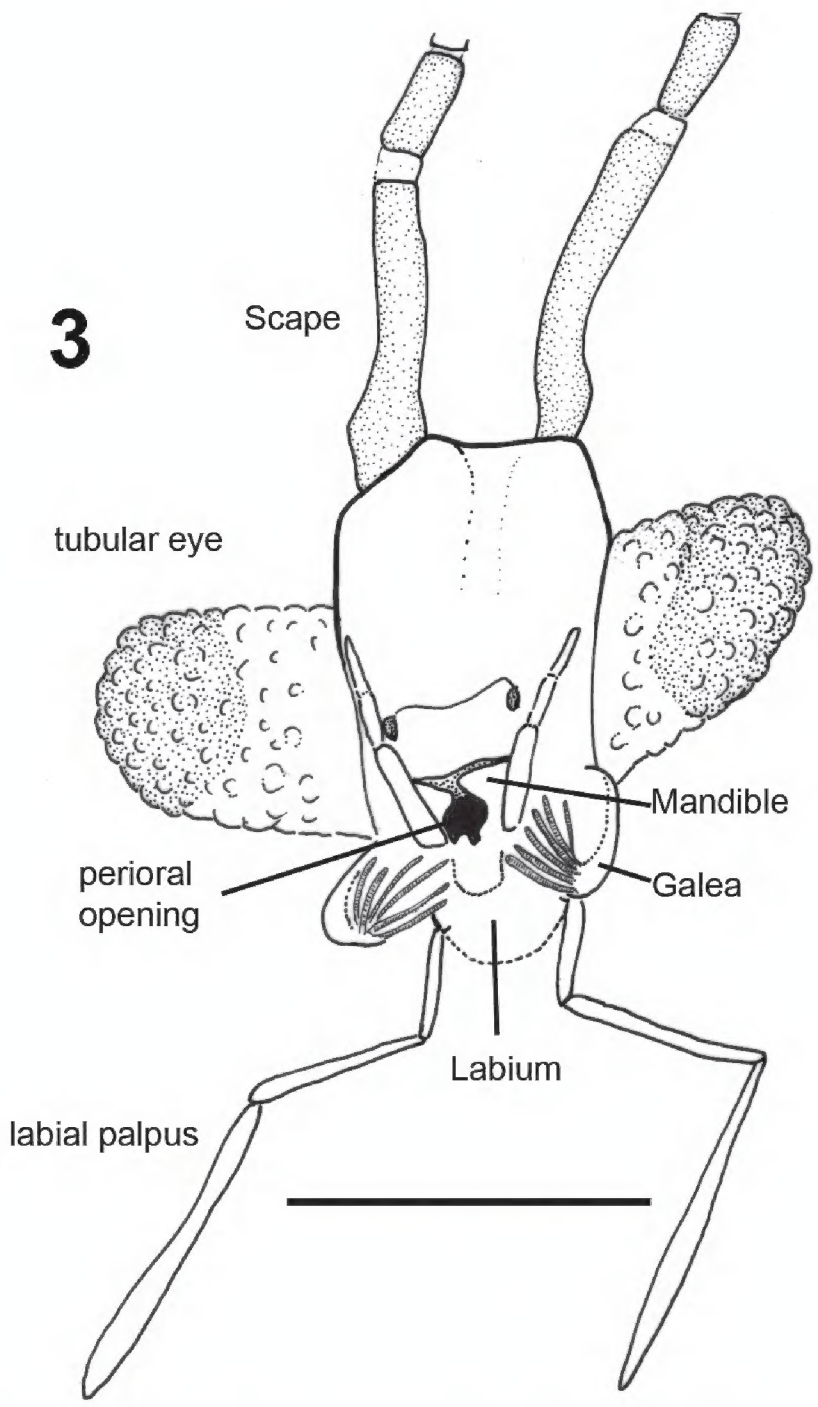
The morphology of the so-far-examined species of the order exhibit a number of characters, which are clearly visible in the amber inclusions. We have identified at least 8 apomorphies and 4 autapomorphies which define Tarachoptera (Wichard and Mey 2021). Together with Trichoptera and Lepidoptera, the Tarachoptera shares seven amphiesmenopteran synapomorphies (Mey et al. 2017a), which are summarized in Table 2. A further character can now be added here resulting from a study of the

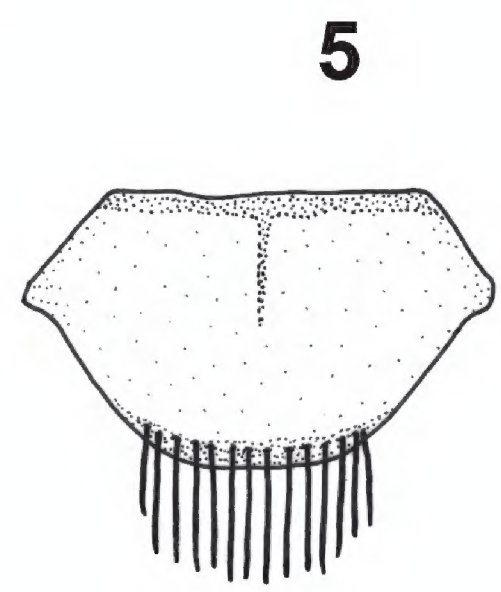
Table 2. Autapomorphies of Amphiesmenoptera, discernible in amber fossils. The majority of characters was proposed by Kristensen (1984), character 8 was introduced by Baixeras (2022).

Number	Autapomorphic characters of Amphiesmenoptera
1	Prelabium fused with hypopharynx, forming eversible haustellum
2	Anal veins of forewings fused, forming one or two basal loops
3	Lower posterior corner of laterocervicale produced towards prosternum
4	Pterothoracic episterna with characteristic suture pattern
5	Wing membrane with extensive covering of setae and/or scales
6	Presence of paired gland openings on sternum V
7	Male abdominal segment IX with tergum and sternum fused, forming a closed ring
8	Campaniform sensilla on apical ends of radial, median, and cubital veins









Figures 1–5. Tarachoptera new species, **1, 2.** *Kinitocelis patrickmuelleri* sp. nov., male holotype: **1.** Head and antennae, dorsal view; **2.** Tip of abdomen, left ventrolateral view. **3–5.** *Tarachocelis emmarossae* sp. nov., male holotype: **3.** Head, frontal view; **4.** Right antenna; **5.** Terminal segment with ventral comb, ventral view. Scale bar: 0.5 mm (**1–4**).

innervation of wings in Lepidoptera by Baixeras (2022). In his study, special attention was paid to the distribution of campaniform sensilla associated with the apices of the longitudinal veins in the fore- and hind wings. These sensilla are presumed proprioceptors providing information on wing movement. The sensilla occur as singletons or doubletons. They are present in nearly all Lepidoptera families including the primitive moth taxa. According

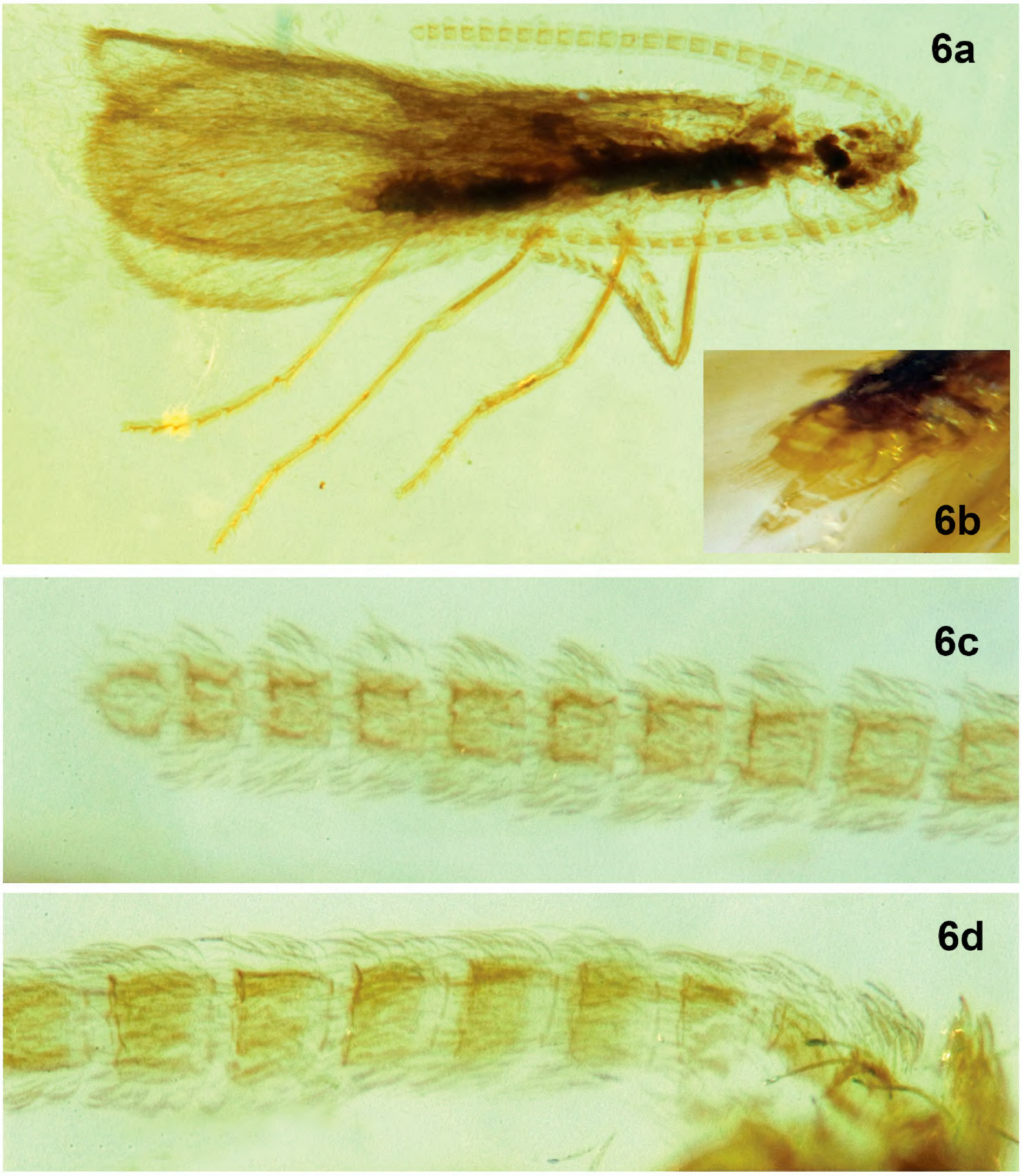
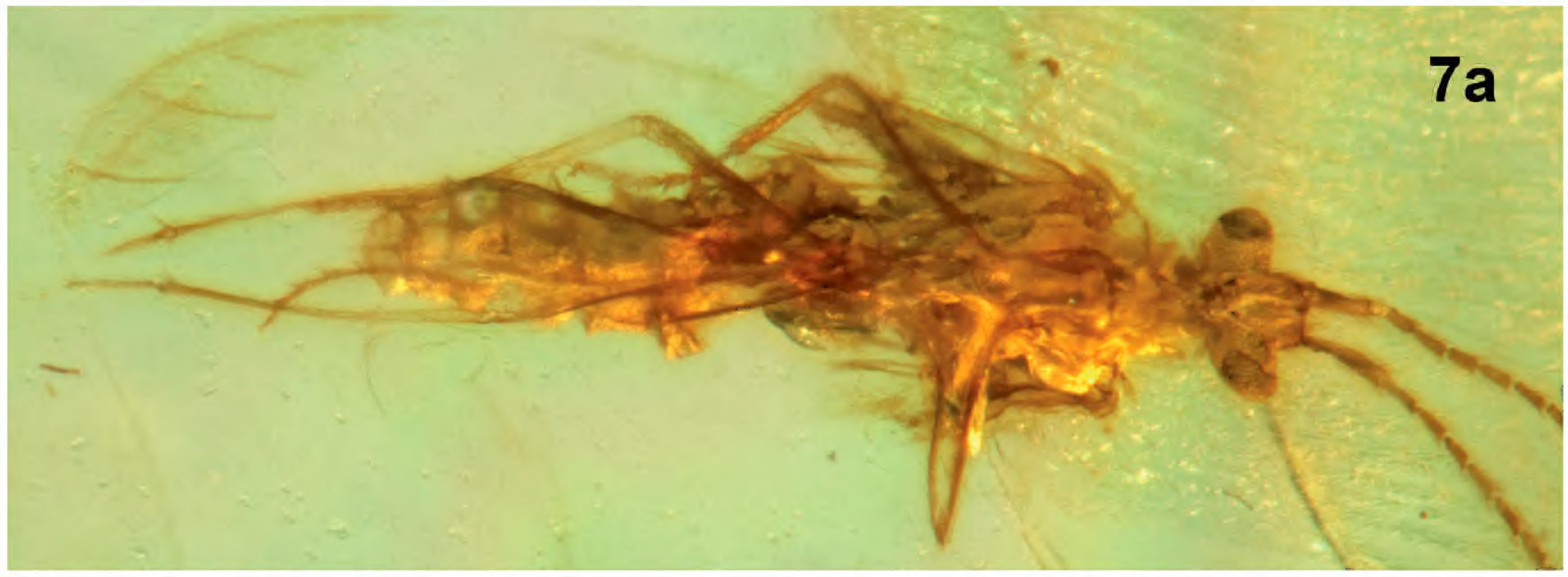
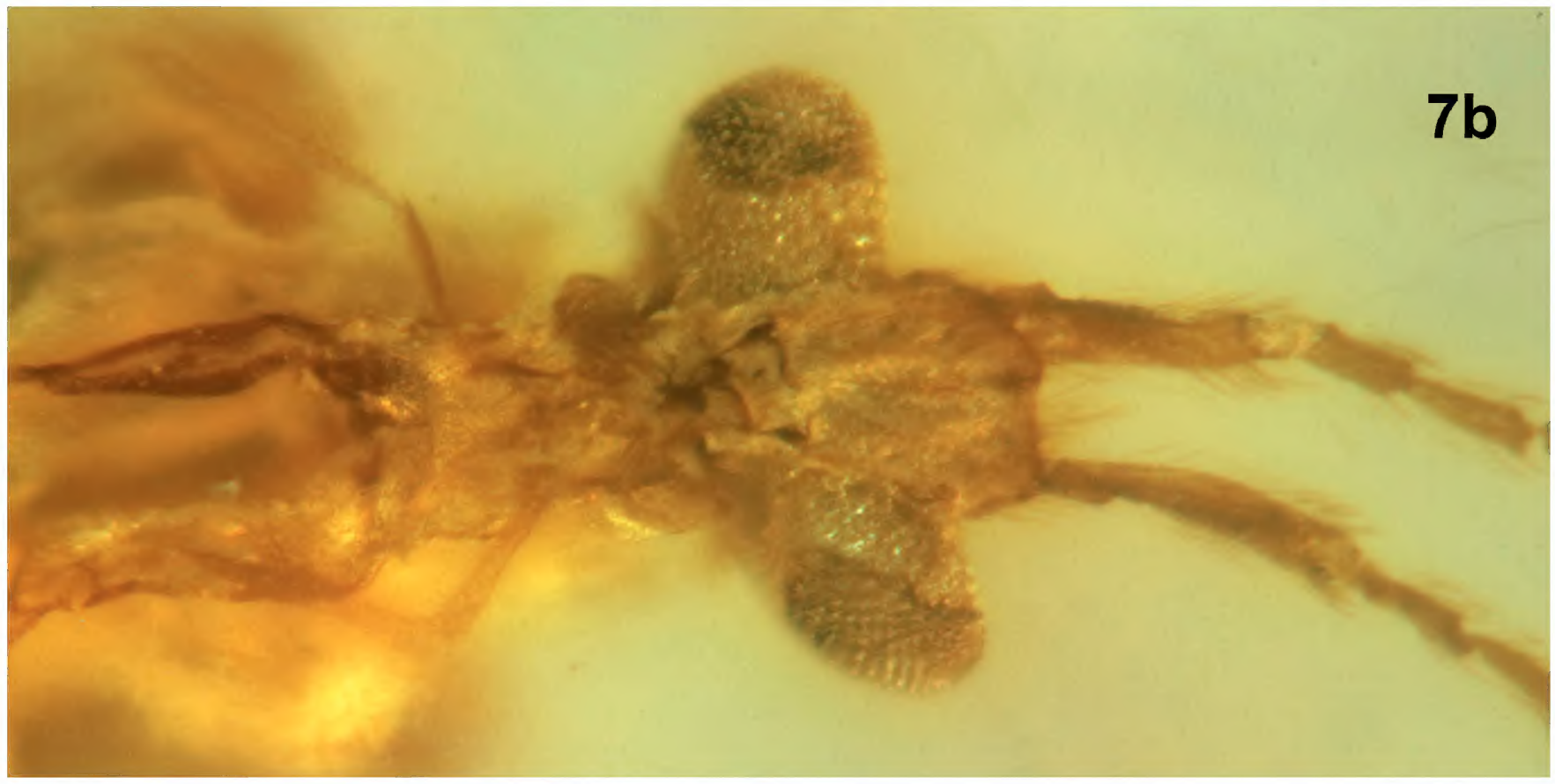


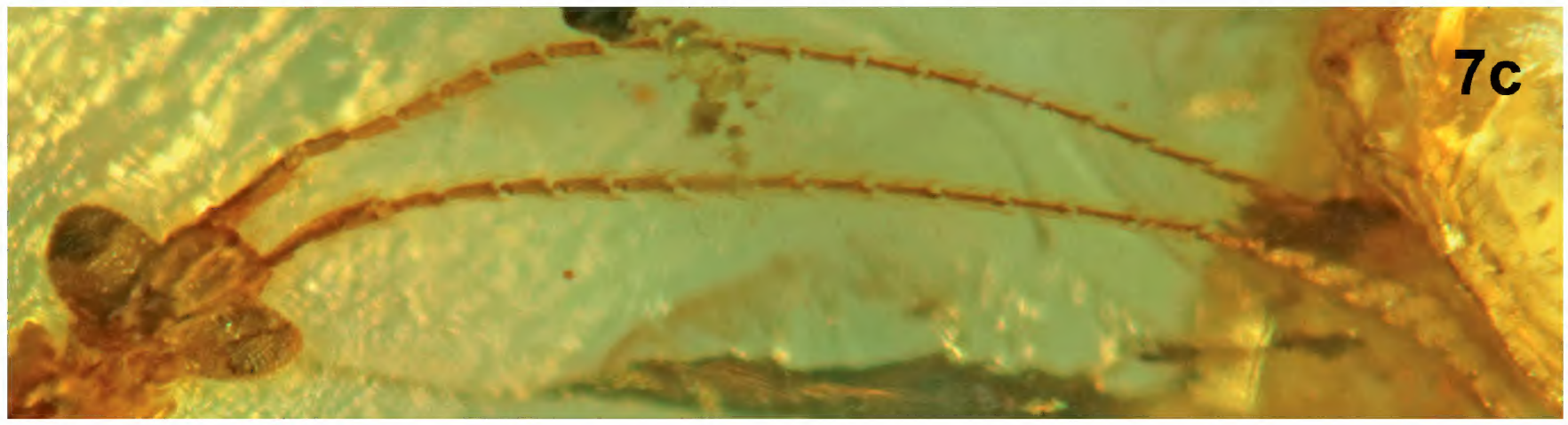
Figure 6. Microphotographs of *Kinitocelis patrickmuelleri* sp. nov., male holotype. **a.** Male habitus, dorsal view; **b.** Abdominal tip, left ventrolateral view; **c.** Apical part of antenna; **d.** Basal part of antenna.

to Baixeras (2022), they also occur in most families of Trichoptera. Johanson (1998) has documented this character for the family Helicopsychidae. In conclusion, the presence of campaniform sensilla on forewing veins is considered a character that belongs very probably to the groundplan of the Amphiesmenoptera clade.

We were able to find this character as occurring in Tarachoptera, too. A male specimen of *Retortocelis minimella* Mey et al. 2018 (deposited in Zoological Research Museum Alexander Koenig, Bonn, Germany, inventory no.: ZFMK-TRI000839 / BUB 4039, ex coll. Patrick Müller) with wings spread and lying closely below the amber surface made an examination by light microscope feasible. Campaniform sensilla were found dorsally at veins R1, R2, and R3 shortly before wing margin. The sensilla are also present on the R veins in hind wings. They occur mostly in pairs, but a triplet seems to occur on forewing R3 (Fig. 8).







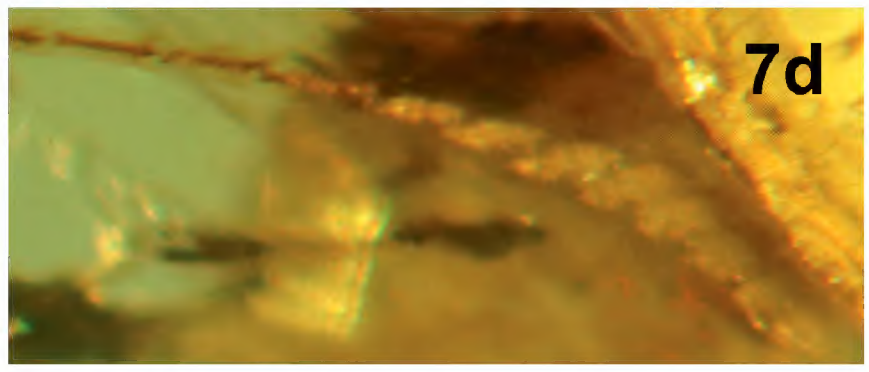


Figure 7. Microphotographs of *Tarachocelis emmarossae* sp. nov., male holotype. **a.** Male habitus, ventral view; **b.** Head and prothorax, ventral view; **c.** Antennae; **d.** Apex of left antenna, ventral view.

Most similarities to Trichoptera and Lepidoptera are symplesiomorphies of the amphiesmenopteran groundplan. Both orders have obviously no common or direct ancestor with Tarachoptera, which was already assumed with the establishment of the order (Mey et al. 2017a: 141). The still unanswered question is: What is the sister group of Tarachoptera and what is the correct position of Tarachoptera within the phylogenetic system of the Amphiesmenoptera clade?

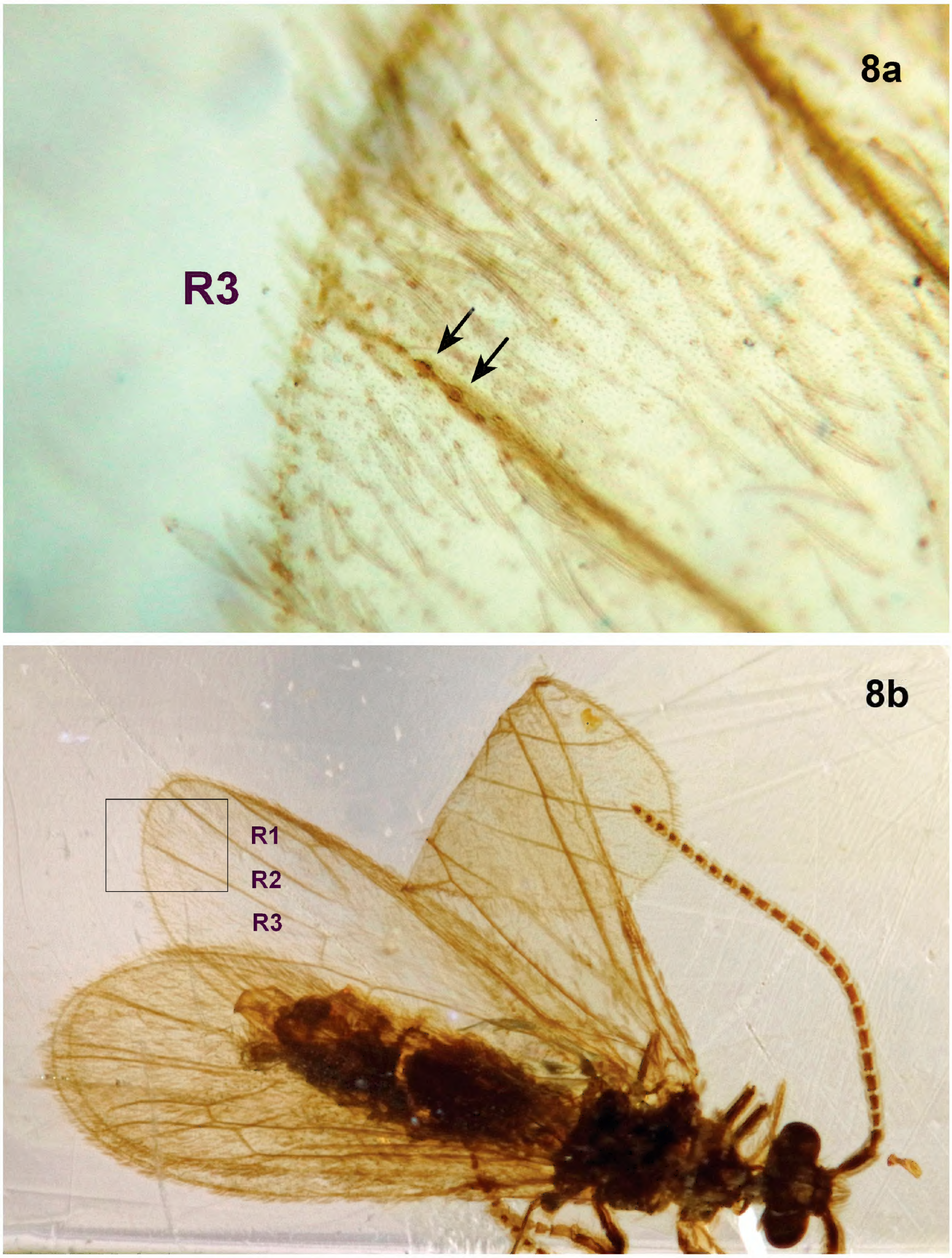


Figure 8. Microphotographs of *Retortocelis minimella* Mey et al. 2018, male (ZFMK-TRI000839 / BUB 4039). **a.** Close-up of forewing R3 with dorsal campaniform sensilla; **b.** Adult, ventral view.

As a first approach, we presented a phylogram in the article where we established the order Tarachoptera (Mey et al. 2017a). This was a simplified picture (Fig. 9) and was intented to demonstrate the distinctiveness of Tarachoptera in contrast to Trichoptera and Lepidoptera. When comparing fossil Tarachoptera with extant Trichoptera and Lepidoptera, we also have to consider the described fossil taxa of Trichoptera and Lepidoptera. The comparative analysis of fossil taxa is a difficult task due to its heterogeneous state of preservation. Moreover,

in nearly all cases, they do not exhibit phylogenetically significant characters, which were established from the study of extant species. Most fossils (with exceptions of those preserved in amber) consist of isolated wings and legs. They were often used for the establishment of new taxa of varying taxonomic rank. However, characters of wing venation play a subordinate role in elucidating phylogenetic relationships between ancestral lines of extant Trichoptera and Lepidoptera (cf. Kristensen 1984; Weaver 1984). According to Kristensen (1984), Willmann (1989), and Ivanov and Sukatsheva (2002) four wing characters might have phylogenetic significance in the basal Amphiesmenoptera clade:

1. The fused anal veins in the forewings forming a single or double loop on the base of the wings. This character separates the taxa of the amphiesmenopteran complex from the related Antliophora (Mecoptera, Siphonaptera, Diptera) and Neuropterida (Rhaphidioptera, Megaloptera, Neuroptera).
2. The number of radial and median veins are reduced to five and four respectively. This trait is an autapomorphy at a very early phase in the evolution of Amphiesmenoptera.
3. The reduction of SC veins in the forewings from several to only one.
4. Anterior cubitus (Cu) apically forked into CuA1 and CuA2.

The very different wing venation of Tarachoptera with reduced numbers of R and M branches in contrast to that of Trichoptera and Lepidoptera, however, demonstrates the importance and utility of this character complex in elucidating phylogenetic relationship at ordinal and subordinal levels.

The large number of descriptions of fossil taxa assumed as belonging to Amphiesmenoptera are difficult to group into a meaningful phylogram, because they are comprising trichopteran and lepidopteran lineages. Ivanov and Sukatsheva (2002) have included all amphiesmenopteran taxa within Trichoptera. This seems not to be tenable anymore, because the placement of Tarachoptera into the current phylogenetic system has to consider the fossil species, which in consequence necessitates a reevaluation of these taxa. The oldest fossils assigned to Trichoptera are dating back to the Permian period and are summarized in the suborder Protomeropina (cf. Ivanov and Sukatsheva 2002). This group was excluded from Trichoptera by Wiggins (2004: 73) and transferred to Amphiesmenoptera, thus representing the common ancestor of both Trichoptera and Lepidoptera.

In contrast to the previous phylogram of Fig. 9, and the cladogram of Wang et al. (2022), which are both bottom-up approaches, we here propose a top-down approach towards integrating Tarachoptera into the amphiesmenopteran clade phylogeny. It is based on cladistic principles, with the search for sister-group relationships of monophyletic clades. The resulting dichotomized cladogram is depicted in Fig. 10. It is not a new hypothesis, but rather a theoretical construct that aims at providing some guidance into the interpretation of known and unknown fossil taxa. We have attempted to identify synapomorphies and attach names of taxa to the various clades. However, this is not an easy task given the poor and heterogeneous information content of newly established taxa in Amphiesmenoptera (cf. Huang et al. 2010; Zhang et al. 2013, 2015). A good and comprehensive knowledge about the richness of the fossil record is a prerequisite for assigning characters and taxonomic names into the cladogram, knowledge, which we do not have at this stage of research.

According to the model in Fig. 10, Trichoptera and Lepidoptera do not have a strict sister-group relationship. Their proper sister-groups have still to be found or defined. The same applies to the Amphiesmenoptera in its traditional sense of being restricted to Trichoptera and Lepidoptera. The sister group of Amphiesmenoptera is unknown, but some of the known fossils might be ascribed to this clade. The Protomeropina represent the most basal group in the amphiesmenopteran clade and include the oldest fossils assigned to this taxon.

The Tarachoptera are grouped in a Tarachoptera clade, distantly related to Trichoptera and Lepidoptera, which is expressed in the placement of this order in a somewhat remote branch of the cladogram.

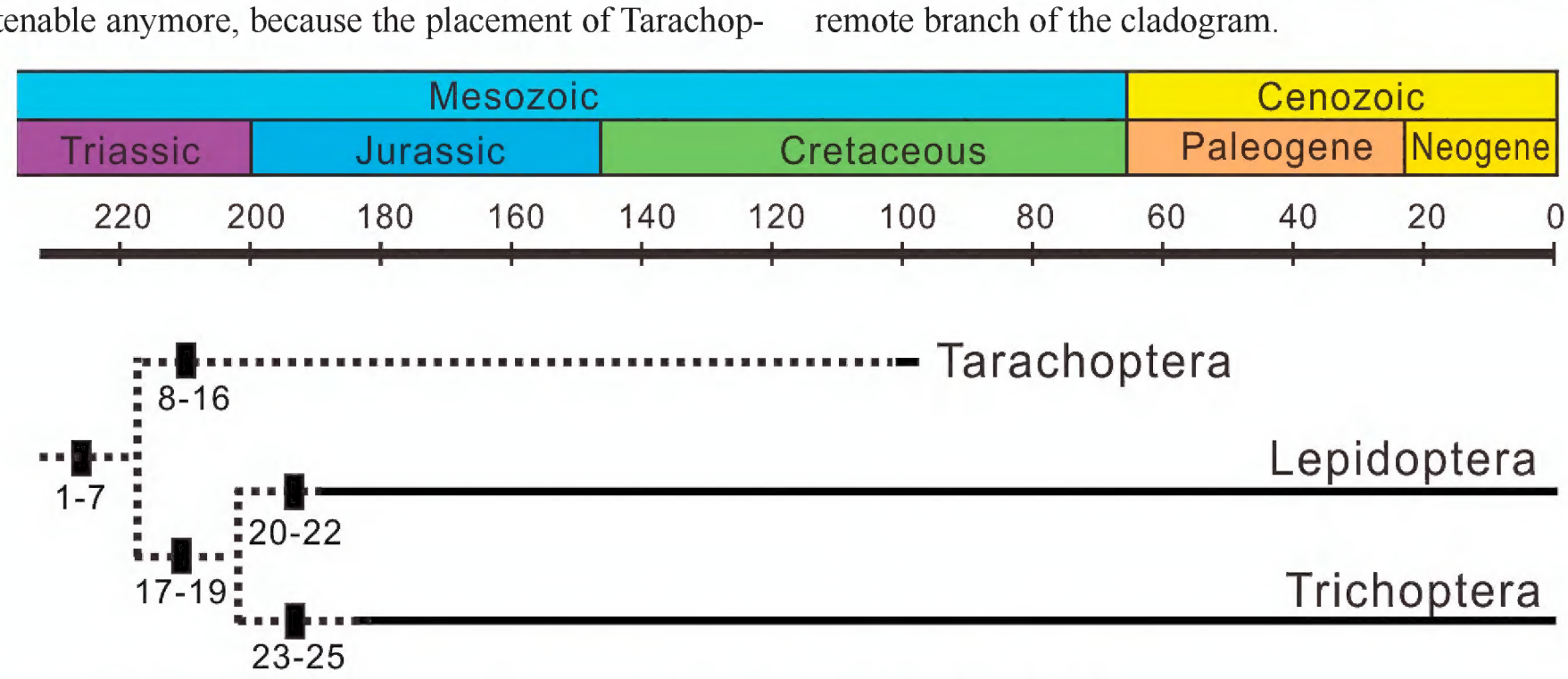


Figure 9. Cladogram of the phylogenetic relationships of Tarachoptera (Mey et al. 2017b).

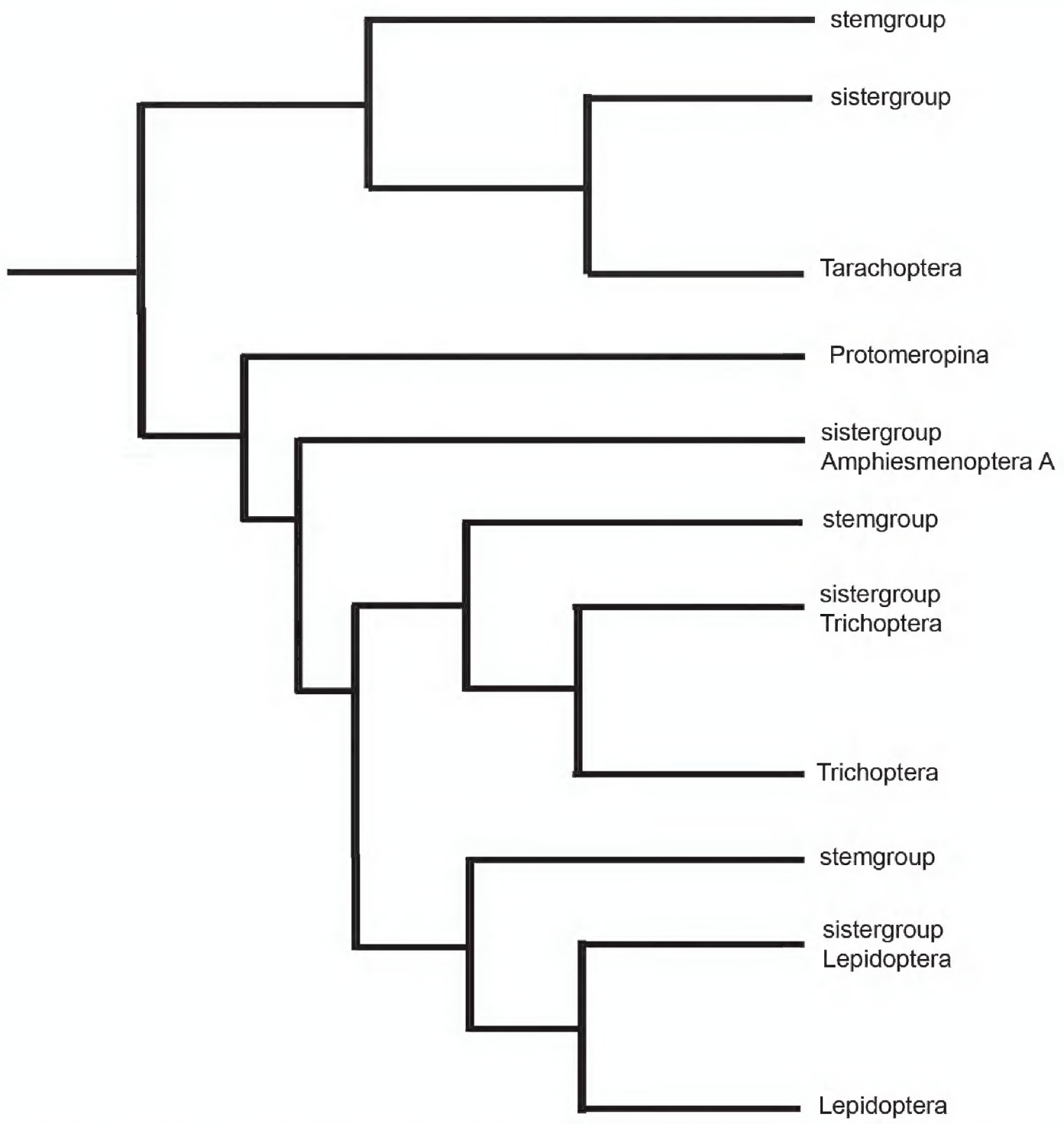


Figure 10. Hypothetical cladogram of phylogenetic relationships of Tarachoptera, Trichoptera, and Lepidoptera.

A major consequence of a future transformation of the theoretical cladogram (Fig. 10) into a substantial hypothesis with distinct taxa certainly will necessitate the introduction of new names on the ordinal and supraordinal level. The term Ampiesmenoptera remains restricted to Trichoptera, Lepidoptera and their common sistergroup termed here as Ampiesmenoptera sensu stricto. In consequence, Tarachoptera cannot be subsumed under Amphiesmenoptera anymore but must be integrated into a new category for which a new name is to be proposed.

Stemgroup taxa of related clades are often difficult to distinguish, and their placement in a cladogram must remain uncertain. Hypothetical, extinct species can be reconstructed by using the plesiomorphic states of the accepted autapomorphies of Trichoptera and Lepidoptera. To give an example, let us consider the haustellum of Trichoptera. It is a composite structure, with the fusion of hypopharynx, labium, and prelabium, constituting an eversible organ. Its formation surely occurred during a long process over several steps that are usually not preserved in the fossil record. In combination with the formation of the haustellum, the morphology of the maxillae and mandibles must also have undergone changes, which are adaptions or expressions of the mode of feeding. The mandibles of modern adults are nonfunctional and their muscles atrophy following adult emergence. Prior to the formation of the haustellum, which allows the uptake of fluids and fluid substances, feeding on plant material as detritivores, fungivores, or even in a phytophagous mode appears to have been possible. The mandibles should have played an important role in any of these modes of feeding. Adult mandibles in the Rhyacophilidae, Stenopsychidae, and Hydropsychidae are still large structures. If they previously remained sclerotized at the adult stage, they may even have allowed a predatory way of life. Caddisflies are known as predators at the larval stage in some families. With regard to families in Neuropterida and Antliophora, where the predatory feeding mode of larvae is maintained to the adult stage, one can imagine a similar mode of life for ancestral caddisflies, flying around as predators with large mandibles and feeding on smaller insects. These hypothetical adult caddisflies with functional mandibles could also have been detritivorous or fungivorous insects, whose aquatic larvae used the same food resource.

Another example can be taken from the Lepidoptera. The complete scaling of the adults, at least on the wings, is an autapomorphy of the order (Kristensen 1984). The plesiomorphic state of this character was probably a more or less advanced stage exhibiting an incomplete scaling. Adult wings with a mixed cover of hairs and scales could

be envisaged, but are not present in the basal lines of Lepidoptera. However, this character is present in species of Tarachoptera, and it seems to be plausible to expect a similar feature as an intermediate state in the ancestry of Lepidoptera.

We can, theoretically, reconstruct several other examples of ancestral, hypothetical species using the plesiomorphic states of apomorphic characters. They might come close to those of the taxa, which belong to the clades of the sister- and stem-groups in the cladogram of Fig. 10. Such species are not known to occur from the fossil record or they are not yet recognized as such. It does not mean that they did not exist. The fossil record is a fragment of the evolutionary history and the discovery of new fossils with hitherto unknown features always bears the potential for new insights into the evolution of morphological characters. Also, the inventory of extant Trichoptera and Lepidoptera on a world-wide scale has still not been accomplished. New discoveries even at the ordinal level appear not altogether as unlikely (Kristensen 1984: 169).

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